Post-release survival of trap-captured spot prawns (*Pandalus platyceros*) declines with increasing air exposure and temperature­

E.M. Atkinson­­1,2,\*, K.M. Ford1, J. Houtman2,4, M. A. Lewis1,2,3,4

1*Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada, [postal code]*

*2Department of Biology, University of Victoria, British Columbia, Canada, [postal code]*

*3Department of Mathematics & Statistical Science, University of Alberta, Edmonton, Alberta, Canada [postal code]*

*4Department of Mathematics & Statistical Science, University of Victoria, British Columbia, Canada, [postal code]*

*\*Author to whom correspondence should be addressed: E-mail:* [emmamargaretatkinson@gmail.com](mailto:emmamargaretatkinson@gmail.com)

*Running headline: Spot prawn survival declines with air exposure and high temperatures*

**ABSTRACT**

*Prawns like to be cold*

*Release them lickety split*

*Back to life at depth*

**KEY WORDS**

fisheries management, spot prawn, post-release survival, population dynamics, marine invertebrates

**INTRODUCTION**

Marine invertebrate fisheries are growing faster than any other group of fisheries in the world, with catches increasing by six-fold since 1950 and double the taxa reported (Anderson et al. 2011). Within that growth, decapod crustacean fisheries are growing faster than any other major group of marine invertebrates (Boenish et al. 2022). Despite the pace of expansion, invertebrate fisheries receive relatively less scientific and stock assessment attention (CITE). This attention is pivotal to stewarding marine invertebrate populations because they play important ecosystem roles (e.g., Eddy et al. 2017, CITE, CITE) and because this trend may be an example of ‘fishing down the food web’ (Pauly et al. 1998; Pinsky et al. 2011) which is accompanied by risks to ecosystems and the human communities that depend on them (CITE). The global pattern of expanding invertebrate fisheries is mirrored on the Pacific coast of Canada where declining finfish fisheries have led to a redistribution of effort towards invertebrate fisheries (Perry et al. 1999) including the spot prawn fishery in British Columbia (BC).

Spot prawns (*Pandalus platyceros*) are sequential protandrous hermaphrodites, beginning their lives as males before transitioning to and reproducing as females. In BC, they are thought to live for four years (Butler 1964). In the spring, brooding females release hatched eggs which spend 2-3 months in a larval dispersal stage before settling and developing as juveniles in shallow waters (Marliave and Roth 1995). Spot prawns spend ~2 years as males before transitioning to females. They breed in the late summer through early fall and females brood eggs through the winter before releasing them the following spring. Timed to begin after most brooding females have released their eggs, the commercial spot prawn fishery is the largest shrimp fishery in BC.

With annual landed values of $33.5-39 million (DFO 2019), the commercial fishery supports over 250 licenses and a growing recreational fishery. While most shrimp fisheries are conducted by trawl with accompanying concerns for their negative ecosystem impacts (Andrew & Pepperell, 1992), the prawn-by-trap fishery represents a rare example of a relatively low-impact shrimp fishery (Boutillier and Bond 2000). The commercial fishery is managed as a derby style fishery, where in-season closures are implemented based on the average number of females-per-trap (the ‘Spawner Index’, Boutillier and Bond 2000) to ensure sufficient spawning females for the subsequent year. An additional management measure was introduced in 1985, implementing a minimum size limit of 30 mm carapace length. Since then, the size limit has increased to 33 mm and commercial traps must comply to a minimum mesh size. These size-based measures are designed to protect the small males in the population who will fertilize females and go on to transition and reproduce as females in subsequent years. Furthermore, the year-round recreational fishery mandates that egged females must not be retained. Despite numerous release-based management measures, the survival of released prawns is not well understood.

[add a paragraph on the body of research on post-release survival in fisheries]

To address the uncertainty in post-release survival of spot prawns caught in trap fisheries, we conducted an in-situ field experiment that evaluated the influence of air exposure, air temperature, and carapace length on the probability of survival after release. [flesh out transition paragraph]

**MATERIALS AND METHODS**

We conducted 23 experimental trials between May 22, 2022 and June 28, 2022 in the Broughton Archipelago, British Columbia, Canada (Fig. 1). A given experimental trial consisted of three components conducted over three days: setting traps for field collection, collecting prawns and conducting the experimental treatment, and processing prawns at the end of the experiment to assess survival and condition. Each trial took 3-4 days to complete (the string of traps to initially collect prawns soaked for 24-48 hours).

EXPERIMENT SET-UP

To collect prawns for a given trial, we set a string of 10 prawn traps (30” tapered stainless steel traps with XX” mesh) baited with pellets (Taplow Feeds Commercial Prawn & Crab bait) within a target depth range (55-110 meters) that aligns with the approximate depth range targeted by commercial and recreational fisheries. Depending on weather conditions and logistics, the string of traps soaked for 24-48 hours before we hauled the traps and began the experimental trial. On the day the trial began, at the trap setting site, we collected air temperature, water temperature (at 0 m and 10 m depths), and water salinity (at 0 m and 10 m depths) using a YSI (YSI Pro30). During some of the trials, the YSI was broken, and we collected temperature and salinity data using a thermometer and refractometer respectively. We hauled the string of traps using a hydraulic pot hauler (10” Hydro-Slave hanging pot hauler powered by 5.5 hp hydraulic power unit). During trap hauling, as each trap came on the boat, we removed any bycatch and emptied the remaining prawns into a small square white bin (10 L, 213 mm x 255 mm x 290 mm) with drilled holes that allowed water to flow through. We placed each white bin in a large fish tote (66 cm x 48 cm x 63.5 cm inside dimensions) filled with seawater (~200 L). This method ensured that until the trial began, prawns experienced minimal air exposure (10-15 seconds as trap was emptied into white bin). After we finished hauling all traps, we assessed how many prawns to assign to each treatment (minimum 35 per treatment, maximum 70 per treatment to minimise density-dependent effects). We haphazardly assigned prawns to one of four or five treatments: ‘immediate release’ or air exposures of 30, 60, 90, or 120 minutes. In circumstances where numbers of prawns was a limiting factor, we did not include the 120 minute treatment. To implement the ‘immediate release’ treatment in an experimentally tractable manner, we hung prawns off the boat in a mesh drawstring bag (insert mesh specs) approximately 20 m below the surface of the water. This mimicked quick release while still allowing for the experimental ‘release’ of prawns from all treatments together in one string of traps. To minimise air exposure, we emptied the prawns of one of the white bins into a solid white bin filled with seawater. We counted out the appropriate number of individuals, using forceps to place a coloured orthodontic ligature tie on the base of the rostrum (Figure X), and placing each prawn in the mesh bag which was submerged in a 20 L bucket of seawater. Once all prawns had been banded for the ‘immediate release’ treatment, we cinched the mesh bag and attached it to a weighted line hanging off the boat to a depth of ~20 m. To begin the air exposure treatments, we removed the remaining white bins from the fish tote at the same time such that all prawns hit the air together. We started a timer for the first treatment (30 minutes) and began to distribute the appropriate number of prawns to each bin, distributing haphazardly by size. For trials with fewer prawns, we allotted one bin for treatment (e.g., ~35 prawns per bin) and for trials with more prawns, we allotted two bins per treatment (e.g., two bins, each with ~35 prawns). For the duration of the treatment time, we kept the bins under the canopy of the boat such that they received no direct sun exposure or direct precipitation. The spatial arrangement of the bins was haphazard with respect to treatment. Choosing different colours for different treatments (the exact colour varied trial to trial), we applied coloured bands to the rostrum of each individual prawn. As the timer for a given treatment went off, we emptied the prawns of a certain band colour into a weighted mesh bag and clipped it to the hanging line such that it descended to hang with the other treatment bags at ~20 m. At the end of the final treatment (90 minutes or 120 minutes), we placed the final group of prawns in a mesh bag hung off the side of the boat such that all treatments experienced the process of being lowered and raised in a mesh bag. Finally, we raised all the bags at the same time and distributed the prawns from all treatments across six baited prawn traps with the tunnels tied shut such that prawns could not escape. To avoid confounding treatment effect with trap effect, we distributed some prawns from each treatment to each trap such that traps contained a mix of all treatments (the coloured bands facilitated mixing prawns without losing information on treatment). Once prawns had been distributed, we closed the traps and reset the string of six traps in the same location and depth they had been hauled from initially. For each trial, we timed the length of time it took from the trial ending (mesh bags coming out of water) to the final trap hitting the water during re-setting.

EXPERIMENT WRAP-UP

Approximately 24 hours after we conducted the experimental treatment, we returned to the re-set string of traps to end the trial. We followed the same procedure as at the beginning of the experiment, collecting temperature and salinity measurements before re-hauling the string and placing the contents of each trap into a white square bin which we kept in the seawater-filled fish tote.

After re-hauling the string, we emptied one square bin (i.e., one trap’s worth of prawns) at a time into a sampling tray and collected the end-of-trial data. For each individual prawn, we recorded their band colour, stage (juvenile, male, transitional, female, egged female, or spent female), and their carapace length as well as whether they were alive, dead, or scavenged. We considered a prawn dead if their gill filaments were not moving at all (i.e., the individual was no longer breathing). A ‘scavenged’ prawn referred to an individual that was dead and missing some body parts. We returned dead and scavenged prawns to the ocean. As they were counted and measured, alive prawns were transferred from the sampling tray to a mesh bag submerged in a 20 L bucket of seawater. After processing a single trap, the mesh bag of live prawns was hung off the boat at 20 m to maintain the prawns as close to their initial condition as possible.

ASSESSING REFLEX BEHAVIOURS

After collecting survival data for all traps, we assayed each live prawn for a suite of ten reflex behaviours, based on the approach outlined in (Stoner 2012) that developed a set of ten reflex behaviours in spot prawns that cumulatively predicted long term survival in the lab. Processing one trap’s worth of prawns at a time, we assessed each prawn for how many of the reflex behaviours they displayed, resulting in a cumulative score that could range from 0-10. Here, a score of zero indicates a prawn that is alive but displays no other behaviours (poor condition) and a score of ten indicates a prawn that is alive and displays all assessed reflex behaviours (good condition). After we finish assessing the reflexes of the live prawns, we remove their nose band and return them to the ocean.

STATISTICAL ANALYSIS

To evaluate the influence of air exposure, air temperature, and carapace length on the post-release survival of spot prawnscaptured in trap fisheries, we used generalized linear mixed-effects models (GLMMs) that accommodate the hierarchical structure of the experiment and the non-linear distribution of the data. Our response data consist of 0 (dead or scavenged) and 1 (alive) so we used a binomial error structure to model the probability of survival. We included a random effect on the intercept for unique trap-within-trial to account for the shared variation within a trap of a given trial (where the number of random effect levels corresponds to the number of trials multiplied by the number of traps).

In some cases (488 of 5053), we excluded data from prawns for which either treatment group or carapace length was unknown. A small portion of the prawns (273) lost their coloured band during the release stage of the experiment (Table 1). As the band colour denoted treatment group, prawns that lost their band could not be assigned to a treatment. We considered the possibility that small prawns may have been more likely to lose their band. To ensure we would not confound our results, we compared the size distribution of these prawns to that of the prawns that retained their band (Appendix 1). There was a statistically significant difference between the two groups (T=3.25, *p*=0.0013), however the difference was very small (1 mm, 3%). We therefore excluded these individuals from the final dataset. We excluded an additional 215 prawns that had damage on their carapace such that we could not measure length accurately.

We considered how the loss of prawns during the experiment may have influenced our results. We lost prawns in two ways: through the mesh of the bags used during the treatment stage or through the mesh of the traps during the release stage of the trial. We could not determine whether these individuals survived the treatment or not. To investigate whether there was a bias in prawn loss (i.e. if either dead or living prawns were more likely to be lost), we evaluated the percentage of prawns lost in each treatment. We found that, on average, more prawns were lost from treatment groups with longer air exposure (Figure X). To evaluate the influence of the potential bias in prawn loss, we simulated four scenarios for prawn loss: no prawns lost, only dead prawns lost, only surviving prawns lost, dead and surviving prawns lost at equal frequencies. We evaluated the difference in survival estimates among the four scenarios to address whether loss of prawns could confound our interpretation of how survival did or did not differ across treatment groups. We found that for a typical percentage of prawns lost (20%) (Figure X), the effect on the estimated percentage of prawns that survived was minor (maximum 6% for most trials) (Figure X) even if we lost living or dead prawns more frequently.

We took a model selection approach to evaluate the relative importance of three fixed effects and their two-way interactions: time out of water, air temperature, and carapace length. In total, we considered a suite of 18 candidate models estimating the probability of prawn survival ~24 hours after release (Table 2). All models included a normally distributed random effect on the intercept to account for variation in the probability of survival across trials and traps. The random effect includes 123 levels, accounting for 21 trials and 6 traps in most trials (Table 1). We expected survival may vary by trial and trap because location, time, and orientation on the ground varied between trial and trap. We conducted all analyses in R (R core team 2023). For completeness, we fit the models in two ways: Gaussian Quadrature (10 points) with lme4 (Bates et al. 2015), and Laplace approximation with glmmTMB (Brooks et al. 2017). To prioritise simplicity and interpretability, we compared models using Bayesian Information Criterion (BIC) (Table 2).

**RESULTS**

The 23 experimental trials included 5,052 prawns encompassing juvenile through female life stages (Figure S2). Due to the timing of the experimental period, we did not have access to egged or spent females to include in the experiment. The majority of the prawns were male or transitional stage and prawn carapace length ranged from 18.0 mm to 52.36 mm (Figure 4). Air temperature varied throughout the experimental season with trials conducted in as cool a climate as 10.7oC and as warm as 25oC. We attempted to maintain as constant as possible high salinity conditions which required pumping water from below the freshwater layer during the freshet. The seawater that we kept prawns in during the experiment ranged from 24.5 ppt to 31.4 ppt, with the exception of two trials which we did not include in the final analysis (trial 11, 21.5 ppt during end-of-trial processing and trial 12, 14.0 ppt during end-of-trial processing).

The post-release survival of spot prawns declined with increasing length of air exposure (Figure 5) and with increasing air temperature (Figure 6). Of the models we fit to determine the best predictors of prawn survival probability, the model including two interaction effects – an interaction between treatment and temperature and between temperature and length – was best supported by BIC (Table 2). The interaction terms suggest that survival probability declines more quickly with time out of water at hotter temperatures and that larger prawns survived relatively worse than smaller prawns at high temperatures (though note that the effect size for the latter interaction was quite small, see Figure X). There was no definitively clear top model, with reasonable support for five models which all fell within 10 ∆BIC of the top model (CITE). The treatment-temperature interaction effect was common across all five top models.

The top model predicts that 32 mm prawns in the ‘immediate release’ treatment have a 94% survival probability in cool conditions (11oC, 95% C.I. = 92-96%), which declines to 78% in hot conditions (26 oC, 95% C.I. = 67-86%). This represents a typical scenario for the commercial fishery where traps must be sorted as they are hauled and prawns under 33 mm must be released. Under cool conditions and when immediately released, smaller prawns (23 mm, the mode length for juveniles) are predicted to survive at a slightly higher probability (96%, 95% C.I. = 95-98%) than larger prawns (39 mm, the mode length for transitionals and females) are predicted survive (92%, 95% C.I. = 89-94%) but this relationship reversed at hot temperatures for which larger prawns are predicted to have a higher survival probability than small prawns (89-94% for 39 mm prawns compared to 52-84% for 23 mm prawns). For an average-sized male prawn (32 mm), predicted survival probability crosses 50% after 95 minutes out of water in cool conditions (10.7 oC) and after 22 minutes in hot conditions (26 oC). Model-averaged predictions of survival probability were very similar to the predictions from the top model so for ease of interpretability we discuss the estimates from the top model in the main text (see Supplementary Material for model-averaged predictions).

The mean reflex score for surviving prawns, on a scale from 0-10, was 8.96 (Figure SX). Based on the reflex-mortality relationships defined in Stoner (2012), we estimated post-experiment mortality of surviving prawns at 6-14% (Figure 5).

**DISCUSSION**

A large proportion of trap-captured spot prawns returned to the ocean near immediately after capture survived the physiological process of being captured and released – we estimated survival probabilities greater than 70% across the range of carapace lengths and air temperatures encompassed by our field experiment. The 24-hour survival probability declined with increasing length of air exposure and the rate at which survival declined with increasing time out of water depended strongly on air temperature. In cool weather, we estimated a probability of survival just under 40% but this dropped quickly with increasing warmth and no prawns survived two hours of air exposure in >25oC weather. Although we did not track survival longer than 24-hours post release, our assessment of reflex behaviours suggests that the majority of surviving prawns were in good condition, indicating possible longer-term survival. Discard mortality in fisheries is an increasingly acknowledged and investigated uncertainty (e.g., ICES 2004; Basti et al. 2010; Wilson et al. 2014; Patterson et al. 2017), but it is relatively less well understood for fished invertebrates and, as far as we are aware, this is the first assessment of post-release survival of spot prawns and one of few assessments of post-release mortality in trap-capture invertebrate fisheries. The broad results of our experiment are generally consistent with previous studies on the discard mortality of other marine invertebrates, including the strong influences of air exposure and temperature on post-release survival. While we expected that spot prawns would fair less well out of water for long periods of time in hot weather, we were surprised by the relatively high survival of individuals released immediately and the high reflex scores for surviving prawns, regardless of air exposure treatment.

Handling, physiological, and environmental factors contribute to the observed patterns in post-release survival of spot prawns. Most of the existing research investigating post-release survival for invertebrate fisheries focuses on invertebrate trawl fisheries and while there is variability in the exact methods and survival estimates, survival estimates tend to be lower for trawl-caught invertebrates than trap-caught. In a paper investigating the survival of mantis shrimp, Lorenzon et al. documented 100% survival of individuals caught by trap in October compared to 0% survival for those caught by trawl at the same time of year (2013). Other trawl-based survival estimates are more optimistic including ~50% survival of mantis shrimp exposed on deck for 10 minutes after a 30 minute trawl (Hill and Wassenberg 1990) and 37-51% survival of Norway lobster subjected to different sorting methods (Mérillet et al. 2018). Within trap-based fisheries, there is evidence that slower hauling speeds contribute to higher survival rates (Basti et al. 2010). Invertebrate species, such as Dungeness crab, which experience intertidal environments during their lives appear to survive at higher rates after release (Yochum et al. 2017). Physiological considerations, including tolerance to significance changes in depth and the metabolic effects of desiccation, influence spot prawns’ ability to survive capture and release.

Although spot prawns are not adapted to direct air exposure as for sub-tidal crustaceans like crab, they settle as juveniles in shallow water (Marliave and Roth 1995) and are known to make nightly diel vertical migrations throughout the water column (Barr 1970). These migrations may confer a baseline physiological tolerance for a wide range of depths. Furthermore, spot prawns and other fished invertebrates do not have swim bladders and thus do not suffer the same barotrauma experienced by, for example, rockfish (CITE). Multiple studies have investigated the metabolic responses of fished invertebrates to capture and air exposure, primarily focusing on desiccation and its associated impacts (e.g., Vermeer 1986, CITE). Because spot prawns and other crustaceans require water flow across their gill filaments for proper respiration, desiccation through air exposure leads to a number of metabolic impacts including a shift to anaerobic respiration and the accumulation of toxic metabolites (Vermeer 1986). While we did not directly measure the metabolic response of spot prawns in this experiment, declining metabolic function is the likely path to mortality for individuals in the longer air exposure treatments. The large negative effect of air temperature on survival is most clearly explained by the increase in desiccation rates of exposed prawns, emphasizing the influence of seasonality and other environmental factors on post-release survival.

Air temperature was a covariate in the five top models comprising 100% of the cumulative model support by AIC (Table 2) and had the strongest effect on the shape of the drop-off in survival with increasing air exposure (Figure 6). On the hottest days (26oC), survival dropped off quickly with air exposure, falling to ~10% estimated probability of survival after an hour out water compared to ~80% estimated probability of survival on a cool day (10oC). This result is consistent with previous studies that have found a strong effect of seasonality (e.g., Giomi et al. 2008; Lorenzon et al. 2013; Mérillet et al. 2018) and intuitive given influence of heat on desiccation rate and associated metabolic function. Although we expected that smaller prawns would survive less well than larger prawns due to their higher relative surface area and possible higher desiccation rates (as in Vermeer 1986), survival was higher at smaller sizes and our top model included a negative interaction effect between temperature and carapace length. While this might be a true ecological effect, it is possible that the difference in survival across size is at least in part an artifact of the experiment itself.

A field experiment provides a more realistic setting to evaluate post-release survival than in the lab; however, there were still several factors we were unable to account for including mechanical damage from handling and from descending in traps, post-release mortality due to predation, and longer term sublethal effects. The relatively higher survival of smaller prawns might be explained by lower susceptibility to injury from handling and from mechanical damage in the traps post-treatment during descent and ascent at the end of the trial. Larger prawns would be subject to higher drag during the hauling process and might have been more likely to get pushed against the sides of traps. Alternatively, despite a lower surface area to volume ratio, larger prawns might have higher absolute metabolic demands that could lead to higher post-release mortality. Further investigation is necessary to understand size-based trends in post-release mortality and the results from this experiment should be interpreted cautiously. To evaluate post-release survival of prawns without needing to recapture released prawns (and the additional complexity of recapture rates) we ‘released’ prawns in traps with the openings closed and thus did not account for additional mortality due to predation. Post-release mortality due to predation is difficult to measure and likely varies depending on predator abundance, descent speed of released individuals, and impairment of predator escape behaviour. There is evidence that air exposure affects the response behaviour of crustaceans including their ability to evade predators at least in the short term (Brown and Caputi 1983; Vermeer 1986; Haupt et al. 2006). Past research has estimated it takes 9-10 seconds for released crustaceans to sink below 1 m (relevant for predation from birds) and found that over 80% of bait set on a vertical drop line were intact of recovery (Hill and Wassenberg 1990). Nonetheless, it is likely that some proportion of released prawns would succumb to predation and further research would be necessary to incorporate this component of post-release mortality. We do not expect that this impacts our estimates of relative survival with increasing air exposure and temperature, but the absolute survival probability should be considered as a ‘best case’ estimate. Finally, it is possible that additional mortality would occur beyond the experimental period considered here. We did not track survival after 24 hours but were able to estimate long-term survival based on an established relationship between reflex behaviour and long-term mortality (Stoner 2012). We estimated that additional long-term mortality of surviving prawns ranged from just over 5% to just under 15% depending on air exposure (Figure 5). While uncertainty remains regarding the precise estimate of post-release survival for spot prawns captured by trap, our results suggest that potential survival could be relatively high given the right handling and environmental conditions. [TRANSITION]

Commercial and recreational fisheries as well as scientific surveys can maximise post-release survival by keeping air exposure brief and taking seasonality into account. The license conditions for the commercial spot prawn fishery specifies that traps must be sorted individually as they are hauled and non-target individuals (under-sized males and egged females) must be released immediately. Compliance with these conditions is likely to minimise mortality due to air exposure and likely also increases the probability that released prawns return to suitable habitat from where they were captured. Compliance and enforcement of this management measure is variable (Coady Webb, *pers. comm.*) and our results underline its importance. The progression of the commercial season typically leads to higher catches of under-sized males as the larger females are fished down (CITE? FIGURE?) and this often coincides with warmer air temperatures in June and July. Releasing under-sized males promptly may be critical to maintaining a healthy population that will subsequently transition and represent the following season’s females. While we did not investigate the influence of salinity in our analysis (all included trials occurred in high salinity conditions), there is evidence that post-release survival declines when release occurs through low salinity layers (Harris and Ulmestrand 2004), which is consistent with our anecdotal observations. Accounting for salinity will be important for commercial fishing that occurs in the heads of fjord systems where there can be a significant low salinity layer. In contrast to the specific license conditions for the commercial fishery, there are no strict regulations for size limits or sorting practices in the recreational fishery, which has grown substantially in recent years. This study suggests that recreational fishers can maximise survival of released egged females and small males through efficient sorting and consideration of warm weather.

[INSERT CONCLUSION PARAGRAPH]

**CONTRIBUTIONS**

E.A. and M.L. conceived the study and designed the experiment. E.A. and K.F. conducted the field experiment. E.A. and J.H. conducted the analysis and generated figures with input from M.L. E.A. wrote the first draft of the manuscript and all authors contributed to the final version of the manuscript.

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